Soil Biology and Biochemistry 123 (2018) 64–73

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

High carbon use efficiency and low priming effect promote soil C stabilization under reduced tillage

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ARTICLE INFO

Keywords:
Soil
Decomposition
Litter
CUE
Enzymes
Priming effect
^{13}C

ABSTRACT

Increasing the accumulation of organic carbon (C) in soils is a crucial challenge both for soil fertility and for climate change mitigation. Heterotrophic microbial communities are key drivers of C cycling in the soil and are influenced by cultural practices, among other factors. However, whether changes in microbial communities in turn affect their C degradation functions is not well understood. Here, we studied the effects of prior soil management on the microbial taxonomic composition and activity of soils amended with wheat litter. Prior soil management was either conventional (CONV) (i.e., full inversion ploughing) or reduced tillage (RT) during a 5-year period in the same loamy soil in northern France. Soil samples taken from the top 5 cm of field plots were incubated with ^{13}C-labelled litter of either flowering wheat or mature wheat for 29 days at 15 °C. We measured the $C\text{-}CO_2$ and $^{13}C\text{-}CO_2$, microbial biomass C (MBC) and ^{13}C, and hydrolytic enzyme activities during decomposition. The initial bacterial and fungal community diversity was studied via high-throughput sequencing of ribosomal genes.

The results showed that the MBC in the RT soil was initially 1.5-fold greater than that in the CONV soil; contrasting taxonomic compositions were also recorded. The soil biotic legacy impacted the degradation functions when the soils were amended with wheat litter. Compared with that in the CONV soil, the enzymatic efficiency of microorganisms in the RT soil increased by 49% and 61% in the presence of mature and flowering wheat litter, respectively. Enzyme efficiency was positively correlated with microbial litter C use efficiency (CUE) ($r = 0.92$, P-Value < 0.001) but negatively associated with the priming effect (PE) ($r = -0.85$, P-value < 0.001) across all soils and litter treatments. These findings demonstrated that the RT soil benefited both from an increase in litter C incorporated in the microbial biomass and from a reduction in soil C loss due to the PE, regardless of the quality of the decomposed litter. Our study indicated that agricultural practices such as RT, which enriches the amount of soil organic C (SOC) in the topsoil layer, can lead to positive feedback against C stabilization functions.

1. Introduction

Plant litter decomposition is an essential process that drives major soil biogeochemical cycles (Kim and Dale, 2004). Better understanding and predicting of carbon (C) fluxes from plant litter to soils via decomposition have been the focus of many studies, but mitigating greenhouse gas emissions and improving soil C stabilization remain a major challenge. At the local scale, under given climatic conditions, drivers of decomposition result from interactions between litter quality and quantity and soil organisms (Wickings et al., 2012; Fanin and Bertrand, 2016; Sauvadet et al., 2017). The amount and quality of C added by litter favour different soil microorganism life strategies. For instance, different microorganisms, such as r- and K-strategists, develop at different stages of litter decomposition; this difference is reflected in changes in resource composition during decomposition, as the most labile forms are used first, leaving a more recalcitrant substrate (Berg and McClaugherty, 2008; Tardy et al., 2015). These successions are reflected by the contrasting nature and amount of extracellular enzymes

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https://doi.org/10.1016/j.soilbio.2018.04.026
Received 20 December 2017; Received in revised form 10 March 2018; Accepted 29 April 2018
Available online 14 May 2018
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produced during decomposition (Šnajdr et al., 2011).

Microbial taxa contribute unequally to extracellular enzyme activities; in general, compared with bacteria, fungi exhibit higher levels of production and complexity (Baldrian et al., 2010). The amount of enzymes required to degrade a similar amount of C, defined as enzyme efficiency by Sinsabaugh et al. (2002), varies according to the litter quality and soil characteristics (Sinsabaugh et al., 2002; Wickings et al., 2012; Fanin and Bertrand, 2016; Lashermes et al., 2016). Microbial community structure can also influence enzyme efficiency. For example, a higher proportion of K-strategists in the soil may result in a higher enzyme efficiency; this higher efficiency is due to a stronger specificity and/or synergistic actions of enzymes with their substrates (Amin et al., 2014; Sauvadet et al., 2016). Assessing enzyme efficiency for litter decomposition is important since the enzymes can also break down soil organic matter (SOM) in addition to fresh litter, thus generating a priming effect (PE) by co-metabolism (Kuzyakov and Blagodatskaya, 2015; Shahbaz et al., 2017). However, to the best of our knowledge, enzyme efficiency and the PE have never been measured simultaneously.

The relative proportion of C used for microbial growth out of that taken up from a substrate, which is called C use efficiency (CUE) (Sinsabaugh et al., 2013), depends on numerous abiotic and biotic factors, including microbial taxonomic composition. More specifically, CUE increases as the proportion of fungi and K-strategists in soils increases (Šťursová et al., 2012). CUE values and their drivers have strong potential implications for C storage in soils, as C converted into microbial biomass plays a crucial role in long-term C stabilization (Cotrufo et al., 2015). While both CUE and enzyme efficiency rely on microbial community taxonomic composition, to the best of our knowledge, they have been studied together only once and in the absence of soils (Lashermes et al., 2016). Concomitantly measuring both parameters may facilitate our understanding of the relationships between the structure and function of microbial communities under changing environments. In arable soils, where increasing C storage is an important challenge, cultural practices can strongly impact the soil microbial community structure and soil C contents (McDaniel et al., 2016; Zuber and Villamil, 2016); however, the impact of cultural practices on microbial resource use efficiency is less known.

Therefore, the objective of this work was to assess if and how changes in the microbial community of a soil induced by differences in arable soil management will have legacy effects on C degradation functions by focusing on enzyme efficiencies and CUE. As such, we used an agricultural site that had a 6-year rotation of annual crops; the site was subject to contrasting agricultural management techniques practised since 2010. Two treatments varying by tillage practices (deep tillage (CONV) and reduced tillage (RT)) were used; these treatments can induce substantial differences in the chemical and microbiological characteristics of the 0–5-cm soil layer (Coudrain et al., 2016). Using high-throughput sequencing of ribosomal genes, we assessed the initial bacterial and fungal taxonomic composition. Afterward, using ^{13}C-labelled wheat litter that varied in chemical composition, we measured the decomposition rate, CUE, enzyme efficiency and the PE during litter C degradation. We hypothesized that (i) microbiological soil legacy impacts CUE, enzyme efficiency and the PE and that (ii) these effects depend on initial litter quality.

2. Materials and methods

2.1. Field experimental site and soil sampling

Our study was conducted at the INRA experimental site of Estrées-Mons, in northern France (49°80′N, 3°60′E). The soil at this site is classified as an Orthic Luvisol (FAO classification) or a Typic Hapludalf (USDA classification). The initial organic C, clay, silt and sand contents of the soil were 8.7 mg C g^{-1} soil, 16.8%, 76.3% and 3.8%, respectively, on a soil dry-weight basis (Bertrand et al., 2006), and the pH (soil H_2O) was 7.5. This site has been cultivated for decades with intensive agriculture and deep tillage (CONV) (25–28 cm depth). Since 2010, the agricultural practices on the soil have differed, notably with the establishment of shallow tillage (7 cm depth). Here, deep tillage and shallow tillage are referred to as CONV and RT treatments, respectively (Coudrain et al., 2016).

Soil samples were collected in spring 2015 from the 0–5-cm layer in three blocks of CONV and RT experimental plots. The soil samples were then passed through a 6-mm sieve, after which the crop residue and soil macrofauna were manually removed. The soil moisture was set to a potential of −80 kPa (corresponding to 200 g H_2O kg^{-1} dry soil). To limit the C mineralization flushes consecutive to soil disturbance (sieving, changes in the soil moisture and air temperature), the soil samples were pre-incubated at 15 °C for one month before the beginning of the experiment. The initial total C, total N, ^{13}C, and mineral N contents were subsequently determined.

2.2. Diversity of bacterial and fungal communities

At the end of the pre-incubation period of the CONV and RT soils, microbial DNA was extracted from 1-g (dry weight) soil samples from each of the three blocks (Terrat et al., 2012). Briefly, the bacterial and fungal community structures were determined by 454 pyrosequencing of the 16S rRNA and 18S rRNA genes, respectively; these genes were directly amplified by PCR from soil DNA extracts, as detailed by Sauvadet et al. (2016). Bioinformatic analyses were performed with GnS-PIPE, which was developed for the GenoSol platform (INRA, Dijon, France), as described previously (Tardy et al., 2015). To efficiently compare datasets and avoid biased community comparisons, the high-quality reads were reduced, and the numbers were homogenized between all samples by random selection close to the lowest datasets (2.865 and 4.863 reads per sample for the 16S and 18S rRNA gene sequences, respectively). The kept reads were then compared for taxonomy-based analysis against the Silva database (version r111) using similarity approaches (USEARCH). Finally, the number of genera and the Shannon index were used as indicators of soil microbial richness and diversity, respectively.

2.3. Litter characteristics

Uniformly ^{13}C-labelled wheat straw was obtained by growing wheat from sowing until maturity in an airtight growth chamber for 5 months under hydroponic conditions using a nutrient solution. The plants were continuously labelled with ^{13}C throughout their growth cycle using $^{13}CO_2$ in bottles (^{13}C isotopic excess of 2.00 atom%) throughout the experimental process, as described by Trinsoutrot et al. (2000). Plant material was collected either at the flowering stage (grown for 71 days at 20 °C) or at maturity (grown for 143 days at 20 °C). The harvested plants were then dried at 37 °C for one week, after which they were kept at room temperature until use. We selected stems of flowering and mature wheat; the stems were cut into 1-cm-long fragments.

At day 0, the total C, ^{13}C and N contents of the flowering and mature wheat plants were measured in triplicate by an elemental analyser (NA 2000, Fisons Instruments, Italy). The initial litter chemical fractions of three replicates of 1.2 g of dry matter (DM) were determined in accordance with the following methods: soluble fraction according to the protocol of Van Soest (Goering and Van Soest, 1970), parietal sugars by acid hydrolysis coupled with high-performance anion exchange chromatography (HPAEC) analysis (Machinet et al., 2011), and lignin content by acid hydrolysis in accordance with the method of Monties (1984). Detailed descriptions of the methods used were reported by Sauvadet et al. (2016). The main characteristics of flowering and mature wheat are presented in Table 1.

Table 1
Biochemical qualities of the litter added. The data are the means of three replicates. Significant differences between litter types were tested with one-way ANOVAs.

	Initial values		ANOVA results	
	Flowering wheat	Mature wheat	F-value	P-Value
C:N ratio	19.7 ± 0.1	81.3 ± 0.8	47596	2.3×10^{-8}
^{13}C Isotopic excess (%)	2.95 ± 0.00	2.91 ± 0.00	1061	5.3×10^{-6}
Biochemical fraction content (% *DM*)				
Soluble fraction	30.5 ± 1.8	17.9 ± 1.6	82	8.2×10^{-4}
Cellulose	15.1 ± 0.9	28.9 ± 1.9	11	0.03
Hemicellulose	17.5 ± 0.9	34.3 ± 2.1	11	0.03
Lignin	12.8 ± 0.2	16.3 ± 0.4	154	2.4×10^{-4}

2.4. Incubation experiment

After one month of the pre-incubation of the microcosms of the CONV and RT soils, the incubation experiment started and lasted for 29 days; the incubation conditions consisted of a temperature of 15 ± 0.5 °C, and the soil water content was fixed at a potential of −80 kPa at 200 g H_2O kg^{-1} soil. Briefly, moist CONV and RT soils (equivalent to 150 g of dry soil) in combination with one of three litter treatments—no litter added (control), flowering wheat litter, or mature wheat litter—were incubated in jars, resulting in six different treatments. Each treatment consisted of three replicates per sampling date; these replicates corresponded to the soil samples taken from the three blocks of the CONV and RT treatments in the field. Flowering and mature wheat litter was added at a rate equivalent to 3 g litter C kg^{-1} dry soil, and the litter and soil were manually mixed together before incubation.

All jars were hermetically sealed during incubation; the air inside the jars was changed regularly via aeration, and the soil moisture was controlled by weighing the jars twice a week and adding sterilized deionized water as needed. At days 2, 4, 6, 10, 15 and 29, we destructively sampled 3 replicates per treatment. The soil + litter mixtures were thoroughly homogenized before being separated into subsamples for microbial biomass C (MBC) and enzyme activity analyses.

2.5. Enzymatic assays

After 0, 2, 4, 6, 10, 15 and 29 days of incubation, enzyme assays were performed on the three replicates in accordance with the procedure of Bell et al. (2013). The activities of two different enzymes involved in the breakdown of plant litter cellulose, β-1,4-glucosidase and cellobiohydrolase, were analysed. Soil slurries were prepared by homogenizing 2.20 g of dry soil in 91 mL of 50 mM tris (hydroxymethyl) aminomethane buffer at pH 7.5 (soil pH) in a blender for 1 min. The enzymatic assays used were fluorometric, and 800 µL of the soil slurry was transferred to 96-deep well (1.2 mL) microplates. 4-Methylumbelliferone (MUB) standard curves (0–100 µM concentrations) were included for one of the three replicates of each treatment and measurement date. We added 200 µL of fluorometric substrate and then incubated the samples in the dark for 3 h at 25 °C. After the plates were incubated, they were centrifuged for 20 min at 1620 g. Then, 250 µL of the soil slurry was transferred from each well into black, flat-bottomed, 96-well plates (into their corresponding wells), after which the plates were scanned using a microplate reader (SpectraMax Gemini, Molecular Devices, CA, USA) at excitation and emission wavelengths of 365 nm and 450 nm, respectively.

2.6. Total C and ^{13}C mineralization

C mineralization was measured using an alkali trap (1 M NaOH) placed on the soil surface. The jars were closed with a lid that prevented the exchange of air with the outside atmosphere. The lids were opened and the traps changed at 2, 4, 6, 8, 10, 12, 15, 17, 21, 25, and 29 days after the start of the incubation. On each date, after being homogenized with NaOH solution, a 15-mL aliquot was sampled, after which the CO_2 trapped within the NaOH solutions was then titrated by continuous flow colorimetry using an autoanalyser (TRAACS 2000, Bran and Luebbe).

To determine the ^{13}C content in each solution, the C-CO_2 was precipitated to $BaCO_3$ by mixing a 10-mL aliquot of each NaOH solution with 5 mL of 20% $BaCl_2$. The solution was then agitated, vacuum-filtered (0.45 µm) and dried overnight at 40 °C. A 1.4-mg aliquot of the $BaCO_3$ precipitate was then analysed by mass spectrometry using an elemental analyser (EuroEA, Eurovector, Milan, Itlaly) coupled to an isotope ratio mass spectrometer (IRMS Delta plus Xp, Thermo Finnigan, Bremen, Germany).

2.7. Total MBC and microbial biomass ^{13}C

The MBC in the soil was quantified in accordance with the chloroform fumigation extraction method described by Vance et al. (1987). After 0, 2, 4, 6, 10, 15 and 29 days of incubation, the biomass C was determined by using amounts equivalent to 25 g of dry soil. The soluble C in the fumigated and non-fumigated soils was extracted with 100 mL of 0.025 M K_2SO_4, after which the extracts were shaken for 30 min at 20 °C. The extracts were then centrifuged (15 min at 6118 g) and stored at −40 °C prior to analysis. The extracted C was determined by persulfate oxidation at 100 °C (Nicolardot et al., 2007) using an autoanalyser (Biotech, Aurora 1030), and the biomass C was obtained from the difference in soluble C between the fumigated and non-fumigated samples using the extraction efficiency coefficient of microbial biomass K_{EC} = 0.38 (Vance et al., 1987). To determine the ^{13}C content of each solution, we first mixed together a 12-mL aliquot of the K_2SO_4 extract and 1.8 µL of 12% HCl for one hour to both lower the solution pH to 2.5 and remove all inorganic carbonates. The solutions were then lyophilized, after which 30 mg of the resultant K_2SO_4-C were analysed by mass spectrometry, using an elemental analyser (EuroEA, Eurovector, Milan, Itlaly) coupled to an isotope ratio mass spectrometer (IRMS Delta plus Xp, Thermo Finnigan, Bremen, Germany).

2.8. Data analyses

The amount of C-CO_2 derived from the litter was estimated from the amount of ^{13}C trapped in the NaOH solution:

$$Litter\ C_{CO2} = Litter\ C * \frac{13C - CO2}{Litter\ 13C} \quad (1)$$

where *litter* C_{CO2} is the amount of C-CO_2 derived from the litter (mg C kg^{-1} soil), *13C-CO2* is the amount of ^{13}C-CO_2 mineralized (mg ^{13}C kg^{-1} soil), *litter C* is the amount of C added to the soil by the litter (mg C kg^{-1} soil), and *litter 13C* is the amount of ^{13}C added to soil by the labelled litter (mg ^{13}C kg^{-1} soil).

The PE was calculated in accordance with the following equation:

$$PE = [C - CO2\ amended - Litter\ C - CO2] - C - CO2\ control \quad (2)$$

where *C-CO2 amended* and *C-CO2 control* are the amounts (mg kg^{-1}) of mineralized C in the soil in the presence and absence of litter, respectively, and *litter C-CO2* represents the litter-derived C. All the C-CO_2 data were cumulative over time from 0 to 29 days.

The neoformed MBC derived from the litter C (i.e., litter C-MBC) is calculated as follows:

$$Litter\ C - MBC = Litter\ C * \frac{13C - MBC}{Litter\ 13C} \quad (3)$$

where *litter C-MBC* is the amount of microbial C derived from litter (mg biomass C kg^{-1} soil) and *13C-MBC* is the amount of ^{13}C in the microbial

biomass (mg biomass ^{13}C kg^{-1} soil). The soil indigenous microbial biomass (i.e., soil C-MBC) was calculated as the difference between the total C-MBC and the litter C-MBC. The metabolic quotient, qCO_2 (mg C-CO_2 mg^{-1} C-MBC day^{-1}), was calculated as either the ratio between the mineralization rate (mg C-CO_2 kg^{-1} soil day^{-1}) derived from soil and the indigenous microbial biomass (soil C-MBC) in the control soil or the ratio between the mineralization rate derived from litter and the C recovered from neoformed microbial biomass in the soils amended with litter (litter C-MBC).

CUE was calculated during the first four days of decomposition, when soil microbes were in their growth phase, with the following formula (Sinsabaugh et al., 2013):

$$CUE = \frac{Litter\ C - MBC}{Litter\ C - MBC + Litter\ C - CO2} \quad (4)$$

where *litter C-MBC* and *litter C-CO2* represent the amounts of C derived from litter recovered from MBC and mineralized from litter (mg C kg^{-1} soil), respectively, after 4 days of decomposition.

Enzymatic activity was calculated as the sum of β-1,4-glucosidase and cellobiohydrolase activities (Bell et al., 2013). The enzymatic activity was also expressed in units per gram of dry soil and per milligram of biomass C. Enzyme efficiency, i.e., the amount of litter C degraded per unit of enzyme secreted (Sinsabaugh et al., 2002), was also calculated during the period encompassing days 0–4 as follows:

$$Enzyme\ \ efficiency = \frac{Litter\ C - MBC + Litter\ C - CO2}{Net\ enzyme\ activity} \quad (5)$$

where *litter C-MBC* and *litter C-CO2* represent the amounts of C recovered from MBC and mineralized from litter (mg C kg^{-1} soil), respectively, and *net enzyme activity* is the difference in β-1,4-glucosidase plus cellobiohydrolase activities in amended and control soils (i.e., in soils amended with and without litter, respectively) after 4 days of decomposition (nmol g^{-1} soil).

Differences between the CONV and RT treatments as well as between flowering and mature wheat were tested by one-way ANOVAs. The cumulative C-CO_2 data only for day 29 were compared; we performed one-way ANOVAs with repeated measures from 0 to 29 days for all the other variables. For each community (bacteria and fungi), composition heterogeneity between the CONV and RT treatments was tested by one-way permutational ANOVAs (PERMANOVAs) (Bray-Curtis, 750 permutations); all the genera whose relative densities were greater than 0.5% of the total bacterial or fungal population were tested. All statistical analyses were performed using the R software (R version 3.1.3) platform and the stats, vegan and scatterplot3d packages.

3. Results

3.1. Initial characteristics of the CONV and RT soils

Five years of RT led to a significantly higher soil total C content in the 0–5-cm layer in the RT (12.0 ± 0.1 g C kg^{-1} soil) treatment than in the CONV treatment (9.8 ± 0.1 g C kg^{-1} soil) (P-values < 0.01, Table 2). In addition, the soil N content and soil C:N ratio were higher in the RT treatment than in the CONV treatment (P-values < 0.001), and the MBC and enzymatic activities were also higher (1.5-fold higher in the RT than in the CONV soils, Table 2). When these differences were expressed relative to the amount of soil total C, they were alleviated but remained significant (Table S1).

Changes in soil tillage also affected the microbial community structure in the 0–5-cm soil layer. Both the bacterial and fungal compositions differed between the RT and CONV soils at the genus level (PERMANOVAs P-values < 0.001). Nonetheless, the CONV and RT microbial diversity were relatively similar, with a Shannon Index of 2.7 ± 0.1 and 2.8 ± 0.0 for CONV and RT, respectively, for the bacterial community and 2.0 ± 0.1 and 2.2 ± 0.1 for CONV and RT, respectively, for the fungal community (Table 3). The results of the study of bacterial communities at the phylum level suggests that the differences between the CONV and RT treatments were mainly due to enrichment in populations belonging to the Bacteroidetes and Proteobacteria phyla and depletion in populations belonging to Firmicutes and Thaumarchaeota phyla in the RT soils. The fungal community in the RT soils was characterized by an enrichment in the relative density of the Ascomycota phylum (29.7 ± 2.4% for RT and 23.3 ± 1.8% for CONV), while the CONV soils exhibited higher proportions of Basidiomycota and Glomeromycota phyla.

Table 2
Main abiotic and biotic characteristics of the soils. CONV: soil from the conventional system; RT: soil from the reduced-tillage system. The data are the means of three replicates. Differences between soils were tested by one-way ANOVAs and are emphasized in boldface when significant (P-values < 0.05).

	Initial values		ANOVA results	
	CONV	RT	F-value	P-Value
Organic C (*g kg^{-1} soil*)	9.8 ± 0.1	12.0 ± 0.1	920.7	**7.0×10^{-6}**
Total N (*g kg^{-1} soil*)	1.3 ± 0.0	1.4 ± 0.0	76.4	**9.4×10^{-4}**
C:N ratio	7.8 ± 0.1	8.3 ± 0.1	30.7	**0.005**
Mineral N (*mg N kg^{-1} soil*)	146 ± 31	161 ± 3	0.006	0.94
MBC (*mg C kg^{-1} soil*)	230 ± 15	347 ± 33	31.1	**0.005**
Dissolved organic C (*mg C kg^{-1} soil*)	11.8 ± 2.1	17.4 ± 2.4	9.5	**0.04**
Enzymatic activities (*nmol g^{-1} soil*)	288 ± 21	426 ± 33	36.2	**0.004**

3.2. C-CO_2 and C-MBC during decomposition

Basal respiration (i.e., without litter addition) was significantly higher in the RT treatment than in the CONV; the recorded rates were 86 ± 19 and 40 ± 7 mg cumulative C-CO_2 kg^{-1} soil, respectively, after 29 days of incubation (P < 0.001) (Fig. 1a). When calculated with ^{13}C, the C-CO_2 derived from litter was higher in response to flowering wheat litter than that in response to mature wheat litter (Fig. 1b). However, for each litter type, the litter C-CO_2 emitted was similar in RT and CONV soils. After 29 days, on average, 934 ± 11 and 723 ± 32 mg C-CO_2 kg^{-1} soil derived from litter were mineralized in the flowering wheat and mature wheat treatments (Fig. 1b), corresponding to 29.4 ± 0.4% and 23.1 ± 0.4% of the added litter C, respectively. We observed a positive PE, corresponding to extra mineralization of soil C; this PE was significantly higher after the addition of flowering wheat litter than after the addition of mature wheat litter (+93 ± 6 and +80 ± 4 mg C kg^{-1} soil, respectively). However, as previously observed for litter mineralization, the PE intensity was similar for both soils for a given litter (Fig. 2a). When expressed relative to initial soil C contents, the PE was higher in the CONV soil than in the RT soil by 33% and 19% in response to flowering wheat litter and mature wheat litter, respectively (Fig. 2b).

Total indigenous microbial biomass (i.e., that derived from soil C) was higher in the RT soil than in the CONV soil (Table 1), both in terms of the amount per kilogram of soil (see section 3.1) and relative to the amount of C present in each soil (28.8 ± 2.8 and 23.5 ± 1.5 mg C-MBC g^{-1} soil C in the RT and CONV treatments, respectively, Table S1). This indigenous C-MBC did not change significantly over time for either litter type (Fig. 1c). The microbial biomass derived from mature wheat litter C (neoformed biomass) was significantly higher in the RT soil than in the CONV soil (P-value < 0.01 from day 2 to day 29), while the microbial biomass derived from flowering wheat litter C did not differ significantly between the two soils (Fig. 1d).

3.3. Microbial metabolic activities

The values of the metabolic quotient, qCO_2, of the soil microorganisms in the control soils did not differ between the CONV and RT

Table 3
Microbial community parameters in the investigated soils. CONV: soil from the conventional system; RT: soil from the reduced-tillage system. The data are the means of three replicates. Differences between soils were tested by one-way PERMANOVAs (750 permutations) based on the Bray-Curtis distances of the main genera relative densities (> 0.5% of the total population). For each phylum, differences between the soils were tested by one-way ANOVAs.

	Initial values		PERMANOVA results		
	CONV	RT	F-value	R^2	P-value
Bacteria			5.22	0.57	0.001
Number of genera	61 ± 0	61 ± 0			
Shannon index	**2.7 ± 0.1***	**2.8 ± 0.0***			
Phylum relative density (%)					
Acidobacteria	4.5 ± 0.4	3.9 ± 0.7			
Actinobacteria	7.0 ± 1.2	8.7 ± 1.5			
Bacteroidetes	**13.5 ± 0.9***	**17.5 ± 1.4***			
Crenarchaeota	4.4 ± 0.4	4.4 ± 1.4			
Firmicutes	**4.4 ± 0.3***	**3.0 ± 0.0***			
Planctomycetes	8.1 ± 0.6	8.0 ± 0.3			
Proteobacteria	**30.1 ± 0.7***	**33.4 ± 1.1***			
Thaumarchaeota	**20.8 ± 2.2***	**14.8 ± 0.3***			
Fungi			6.82	0.63	0.001
Number of genera	26 ± 1	27 ± 0			
Shannon index	**2.0 ± 0.1***	**2.2 ± 0.1***			
Phylum relative density (%)					
Ascomycota	**23.3 ± 1.8***	**29.7 ± 2.4***			
Basidiomycota	**16.4 ± 0.7***	**11.3 ± 1.5***			
Chytridiomycota	7.6 ± 0.4	8.9 ± 2.1			
Glomeromycota	**2.5 ± 0.8***	**1.0 ± 0.4***			

For each phylum, the relative densities that significantly differed (P-values < 0.05) between the two soils are shown in boldface and denoted by an asterisk.

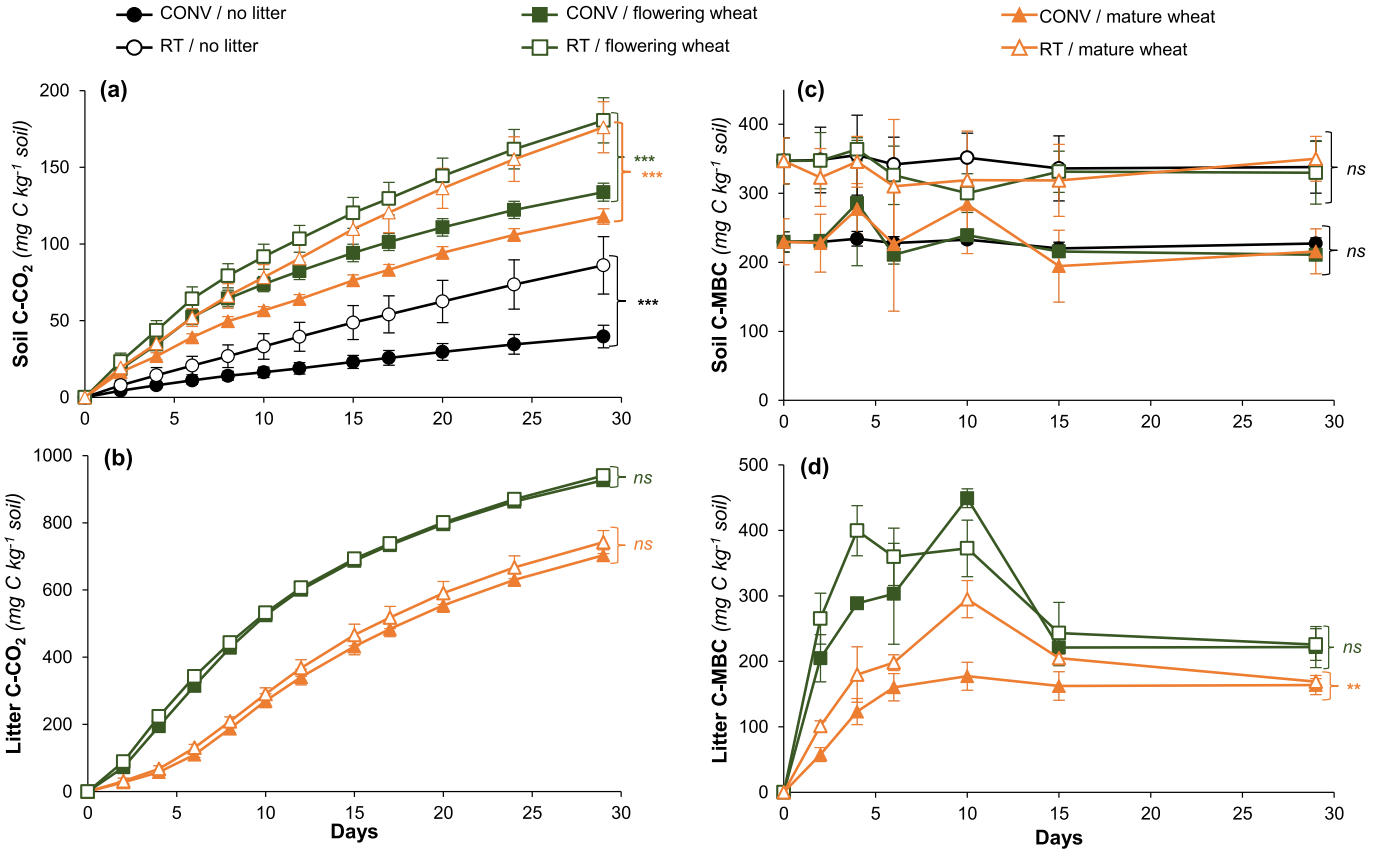

Fig. 1. Cumulative mineralized C ($C\text{-}CO_2$) (a, b) and MBC (C-MBC) (c, d) from wheat litter amendments (a, c) and from the soil (b, d). CONV: soil from the conventional system; RT: soil from the reduced-tillage system. The data are the means of three replicates. Differences between treatments were tested by ANOVA either at 29 days (a, b) or with repeated measures from 2 to 29 days (c, d); ns: P-value > 0.05; **: P-value < 0.01: ns: P-value > 0.05; *: P-value < 0.05; **: P-value < 0.01; ***: P-value < 0.001.

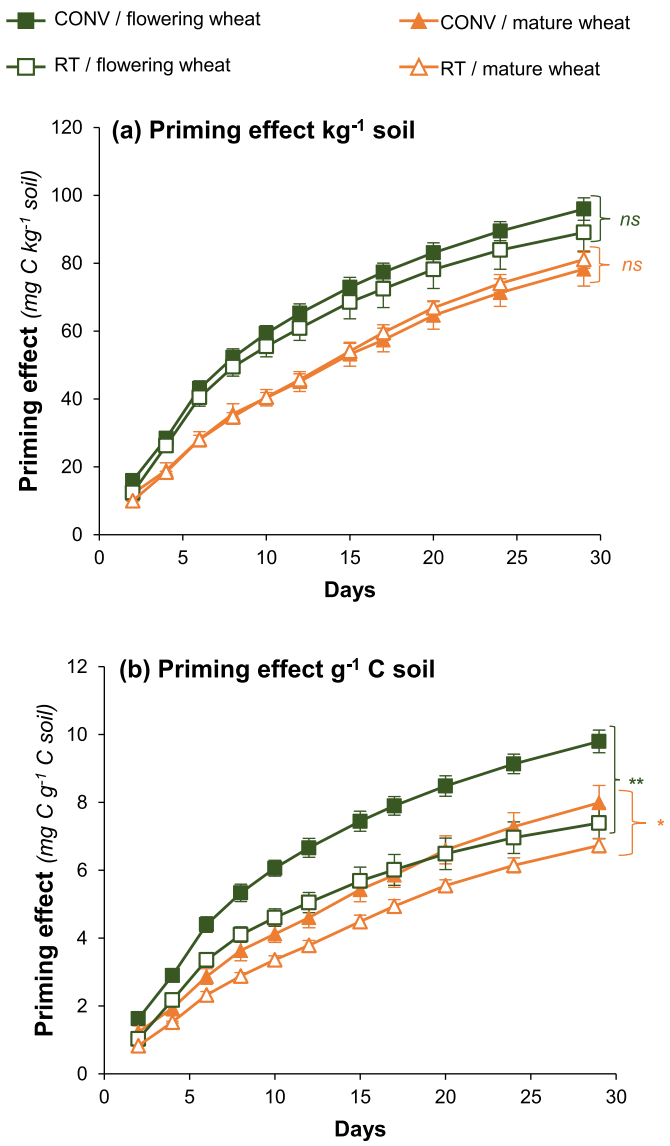

Fig. 2. The cumulative PE by soil mass (a) and organic C mass in the soil (b). CONV: soil from the conventional system; RT: soil from the reduced-tillage system. The data are the means of three replicates. Differences between treatments were tested by ANOVA at 29 days; ns: P-value > 0.05; **: P-value < 0.01.

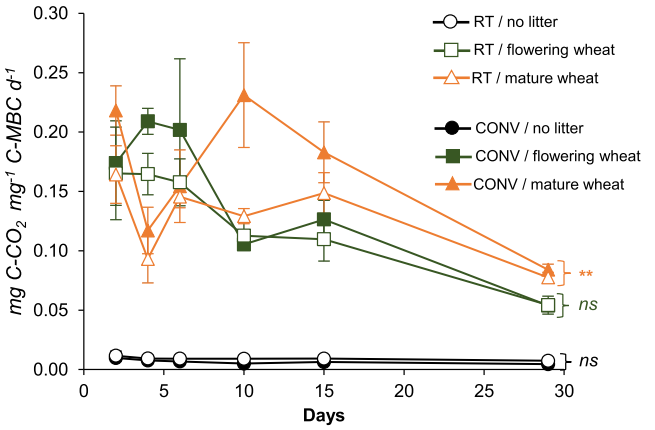

Fig. 3. Metabolic quotient qCO_2 values. CONV: soil from the conventional system; RT: soil from the reduced-tillage system. In the treatments that received litter, the qCO_2 values were calculated from the $C\text{-}CO_2$ and C-MBC derived from the litter; in treatments that did not receive litter, the qCO_2 values were calculated from the total $C\text{-}CO_2$ and C-MBC. The data are the means of three replicates. Differences between treatments were tested by repeated measures ANOVA from 2 to 29 days. ns: P-value > 0.05; **: P-value < 0.01.

treatments (P-value > 0.05, Fig. 3). The addition of mature and flowering wheat litter increased the qCO_2 values of microorganisms growing on litter (neoformed C-MBC) in both the CONV and RT soils. On the other hand, the qCO_2 values of microorganisms growing on the mature wheat litter were significantly higher in the CONV soil than in the RT soil (P-value < 0.01, Fig. 3), while the qCO_2 values of microorganisms growing on the flowering wheat litter were similar between both soils.

The cellulosic enzyme activities in the soils in the absence of litter (control treatments) were always higher in the RT soil than in the CONV soil (P-value < 0.001, Fig. 4a). When litter was added, the enzymatic activities remained higher in the RT soil than in the CONV soil, although the differences between the two soils were greater for flowering wheat litter than for mature wheat litter (P-values < 0.05 and < 0.01, respectively, Fig. 4c and Fig. 4b). In contrast, the amount of enzyme produced per unit of C-MBC, i.e., the specific activity, was similar between the RT and CONV soils under the control and flowering wheat litter treatments (P-values > 0.05, Fig. 4d and Fig. 4e); however, for mature wheat litter, the specific activity in the CONV soil was significantly higher than that in the RT soil (P-value < 0.01, Fig. 4f).

3.4. CUE and enzyme efficiency

The CUE was significantly higher in the RT treatment than in the CONV treatment (P-values < 0.05, Fig. 5a), both for flowering wheat litter (0.64 ± 0.01 and 0.60 ± 0.02, respectively) and mature wheat litter (0.72 ± 0.04 and 0.65 ± 0.01, respectively). The CUE was higher in response to mature wheat litter than to flowering wheat litter for both soils (Fig. 5a).

Enzyme efficiency was significantly higher in the RT soil than in the CONV soil (P-values < 0.05, Fig. 5b) for both types of litter, particularly that of mature wheat (3.58 ± 0.21 and 2.40 ± 0.30 mg litter C degraded $nmol^{-1}$ enzyme in the RT and CONV soils, respectively). In addition, enzyme efficiency was higher in response to mature wheat litter than to the flowering wheat litter for both the CONV and RT soils. As a consequence, the CUE and enzyme efficiency were positively correlated (R^2 = 0.86 and P-value < 0.001, Fig. S1a) on day 4 (Fig. 6). However, we found negative correlations for both CUE and enzyme efficiency (P-values < 0.001, Fig. S1b and Fig. S1c) with the PE calculated during the period from 0 to 4 days (Fig. 6).

4. Discussion

4.1. Effects of soil management practices on microbial community and degradation functions

Five years of different tillage practices led to enrichment in both the SOC content and MBC in the top 0–5-cm soil layer (de Vries et al., 2015; Finn et al., 2017). These differences were caused by the higher dilution of crop residues in the CONV treatment as a result of deep ploughing (Autret et al., 2016). An increase in SOC and MBC contents in the RT treatment likely induced increases in the relative densities of Bacteroidetes and Proteobacteria as well as in the relative fungal density of Ascomycota; these microbial groups are mainly composed of copiotrophic r-strategist populations (Zeng et al., 2016; Ho et al., 2017). Despite the enrichment in r-strategist microorganisms in RT soils, the enzyme activities and the amounts of CO_2 emitted (expressed as units of C-MBC) were similar between the CONV and RT soils in the non-amended control treatments. As a consequence, in the absence of litter C additions, soil C degradation functions appeared to be driven more by the size of the MBC, and in proportion to it, than by taxonomic composition. Such a low linkage between microbial diversity and function in the absence of exogenous carbon input has been reported previously

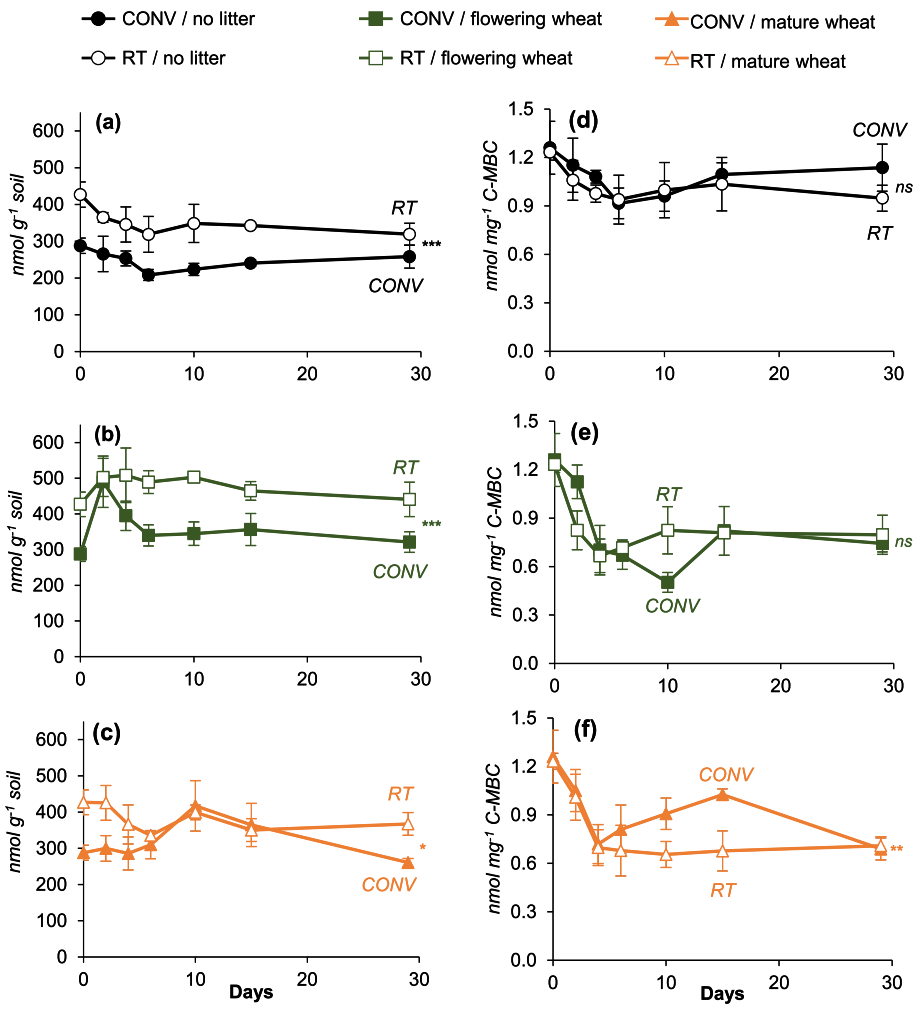

Fig. 4. Enzymatic activities expressed relative to the amount of soil (a, b, c) and relative to the amount of total C-MBC (d, e, f) in soil amended with flowering wheat litter (a, d), mature wheat litter (b, e) and no litter (c, f). CONV: soil from the conventional system; RT: soil from the reduced-tillage system. The data are the means of three replicates. Differences between treatments were tested by repeated measures ANOVA from 2 to 29 days. ns: P-value > 0.05; *: P-value < 0.05; **: P-value < 0.01; ***: P-value < 0.001.

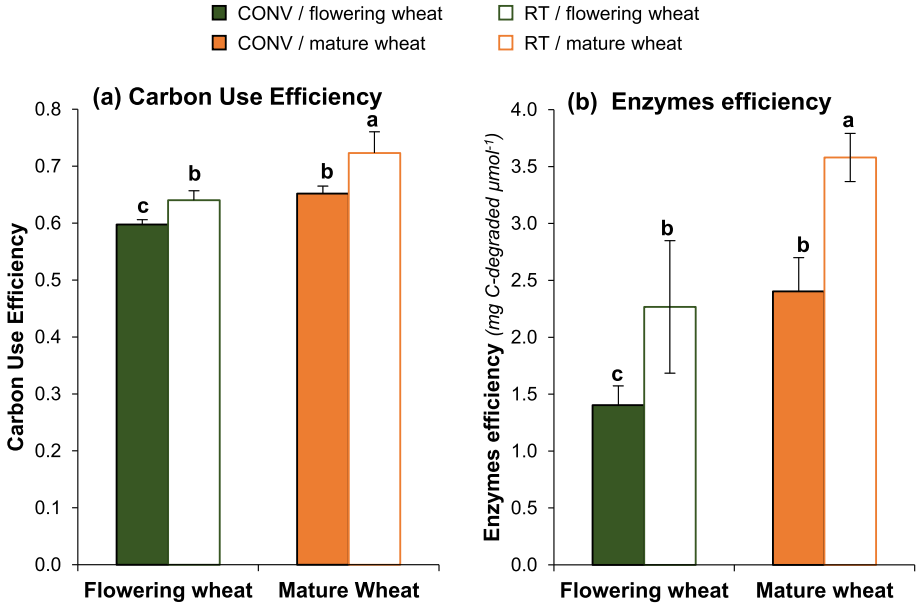

Fig. 5. CUE (a) and enzyme efficiency (b) calculated on day 4 after the addition of flowering wheat and mature wheat litter. CONV: soil from the conventional system; RT: soil from the reduced-tillage system. The data are the means of three replicates. Significant differences between treatments were determined with ANOVA followed by Fisher's least significant difference (LSD) post hoc test. Values that significantly differ (P-value < 0.05) are marked by different letters.

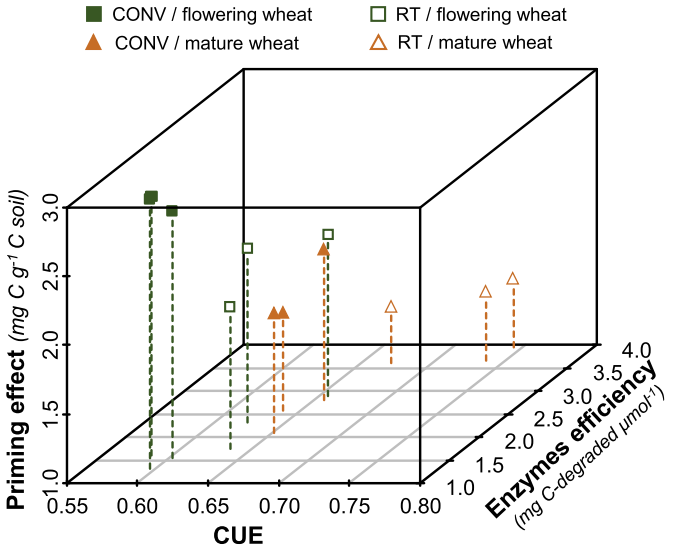

Fig. 6. Relationships between CUE, enzyme efficiency and the PE after 4 days of decomposition. All the treatments that received litter addition (CONV and RT treatments with either flowering or mature wheat addition) are represented (n = 12).

for N-cycling activities (Philippot et al., 2013).

On the other hand, when mature wheat litter was added, decomposition generated more microbial biomass derived from litter C in the RT soil than in the CONV soil for the same amount of litter C-CO_2 mineralized. This result increased the CUE in the RT soils after 4 days. Our results imply that the relatively higher CUE of the heterotrophic biomass is associated with soil that has a higher soil organic C (SOC) and MBC (RT soil), confirming the results of Kallenbach et al. (2015) and Sinsabaugh et al. (2016). This result also suggests that practices favouring SOC accumulation may benefit from microbial positive feedback via increased CUE.

In addition to higher assimilation efficiency, compared with the CONV soil, the RT soil had also lower respiratory costs (lower qCO_2 values) and lower enzyme biosynthesis rates (lower enzyme specific activity) during mature wheat decomposition. We assume that, given the relatively low microbial energetic investment in the RT soil needed to obtain similar litter C degradation rates as those in the CONV soil, there is a correspondingly higher enzyme efficiency in the RT soil than in the CONV soil. For the first time, we show that enzyme efficiency is tightly linked to CUE in soils (both were higher in the RT soil than in the CONV soil). This finding indicates that a microbial community that is more efficient at C assimilation can produce enzymes that are more specific to target a substrate. The energy consumed during the production of enzymes cannot be used for biomass production, as suggested by Lashermes et al. (2016); therefore, the production of highly efficient enzymes allows a higher CUE, as observed in the RT soil amended with mature wheat litter.

We also observed that the higher enzyme efficiency in the RT soil than in the CONV soil was reflected by a lower SOC loss due to the PE. Since the CONV and RT soils mineralized the same proportion of SOC in the control soils when no litter was added, we conclude that the difference in the PE observed between the two soils were not caused by differences in the degradability of the SOC or by the accessibility of the SOC to decomposers. Two known mechanisms drive the PE: nutrient mining and co-metabolism activity (Kuzyakov and Blagodatskaya, 2015; Razanamalala et al., 2018). Since both the CONV and RT soils had high mineral N content, nutrient mining was unlikely; therefore, co-metabolism was likely the main cause of the PE in our experiments. To the best of our knowledge, the co-metabolic PE and enzyme efficiency have seldom been measured simultaneously; their negative correlation provides useful insight into the mechanisms governing SOC loss by the PE. Compared with that in the RT soil, the lower enzyme efficiency in the CONV soil translated into more extracellular enzymes produced and released into the soil at the same level of litter C decomposition; the consequences of this translation therefore increase the probability of both "meeting" (enzyme-substrate association) and mineralizing soil C more in the CONV soil than in the RT soil. This hypothesis will need to be tested on a wider range of soils and C resources. If this hypothesis is confirmed, then measuring enzyme efficiency, which is relatively easy to perform *in situ*, could be used as a proxy for the PE.

4.2. Functional differences between soils affected by litter quality

Comparing flowering wheat and mature wheat litter allows the understanding of how the nature of the resource to be decomposed affects the functional differences between CONV and RT soils. Considering the high importance of litter quality on microbial functioning (Cleveland et al., 2014; Fanin and Bertrand, 2016), it was expected that the most labile litter used in this experiment (flowering wheat) would increase the decomposition rate in both soils, which is in agreement with many studies (Jensen et al., 2005; Berg and McClaugherty, 2008). Similar to the observations involving mature wheat litter, flowering wheat litter decomposition induced a higher CUE, higher enzyme efficiency and lower PE in the RT soil than in the CONV soil. Nonetheless, the differences between the two soils amended with flowering wheat litter were lower than those between the same soils amended with mature wheat litter. The increase in microbial investment in energy for enzyme production (revealed by higher qCO_2 values and higher enzyme specific activities) observed in the CONV soil amended with the mature wheat litter, as previously discussed, was not observed when the same CONV soil was amended with the flowering wheat litter. Thus, despite having grown the same crops for 5 years, changing the tillage depth and hence the concentration of crop residues redirected the CONV and RT soil microorganismal energy investment towards the degradation of recalcitrant litters.

The ability of microbial communities to efficiently degrade crop residues of different qualities was thus central to explaining both the CUE and PE. The influence of litter quality on PE has been increasingly interpreted through its impact on microbial enzyme synthesis (Blagodatskaya and Kuzyakov, 2008; Blagodatskaya et al., 2014; Chen et al., 2014; Loeppmann et al., 2016). Our results suggest, for the first time, that enzyme efficiency may be a better indicator than enzyme activity to evaluate and better understand the priming effect. Similarly, the substrate quality effect on the CUE was also mainly attributed to their influence on enzymatic synthesis in models but mainly without measuring them (Frey et al., 2013; Allison, 2014). Our results confirm our interest in including enzyme-substrate reactions in microorganism-based CUE models and provides experimental data that may be used for their parametrization. Thus, until now, direct relationships among the ability to degrade recalcitrant litters, CUE and enzyme efficiency were mainly overlooked and rather a priori attributed to the microbial community structure.

The high CUE and high enzyme efficiency that were observed in the RT soil are commonly associated with microbial communities dominated by specialized taxa (Fanin and Bertrand, 2016), which are often referred to as K-strategists (Ho et al., 2017). However, the differences observed in the initial CONV and RT microbial community compositions (before litter addition) did not support this assumption, as the RT soil, which had the highest CUE and enzyme efficiency, was initially enriched in r-strategists. However, in this experiment, the CUE and enzyme efficiency were calculated during the first 4 days of litter decomposition; during this initial phase of decomposition. r-strategist populations have been shown to dominate microbial communities because of the preferential depletion of labile compounds within litter

(*e.g.*, Tardy et al., 2015). On the basis of this assumption, K-strategists of the neoformed biomass should not have been major players during this early period and consequently should not be responsible for the high CUE and enzyme efficiency observed in RT soil amended with wheat litter. Therefore, we conclude that, despite being considered mostly functionally redundant, r-strategists exhibited contrasting functions between the CONV and RT soils (*e.g.*, Ho et al., 2017).

5. Conclusion

The changes in soil and microbial properties induced by 5 years of contrasting tillage management practices applied to the field did not impact the biological functions of SOC mineralization within the time scale of the study. However, after the addition of wheat litter, these differences impacted important functions of the heterotrophic microbial biomass, including microbial CUE, enzyme efficiency and the PE, confirming the existence of a legacy effect of prior soil management. We believe that the microbial CUE and enzyme efficiency of soil microorganisms, both of which were higher under RT management than under CONV management in the sampled soils could help explain the increase in SOC content observed in such situations in the long term. This greater accumulation of SOC in RT situations might also be favoured by reduced susceptibility of the soil to the PE as a result of higher enzyme efficiency (and, thus, lower enzyme investment) and lower co-metabolic degradation activity. Compared with those in the CONV soil, resource use efficiency and the PE in response to both flowering and mature wheat amendments were higher and lower in the RT soil, respectively. Furthermore, functional differences between the soils were higher in response to mature wheat litter amendment than to flowering wheat litter amendment, suggesting that the microbial community in the RT soil was better suited to degrade efficiently recalcitrant litters than was the CONV soil.

Acknowledgements

The present study was funded through the INRA Department of Environment and Agronomy and the SOFIA project (ANR Agrobiosphere, ANR-11-AGRO-0004), which provided a doctoral grant to Marie Sauvadet. The authors thank S. Millon, O. Delfosse and V. Nowak for their participation in the laboratory analyses.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2018.04.026.

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